The impact of inter-annual rainfall variability on African savannas changes with mean rainfall

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ABSTRACT

Savannas are mixed tree-grass ecosystems whose dynamics are predominantly regulated by resource competition and the temporal variability in climatic and environmental factors such as rainfall and fire. Hence, increasing inter-annual rainfall variability due to climate change could have a significant impact on savannas. To investigate this, we used an ecohydrological model of stochastic differential equations and simulated African savanna dynamics along a gradient of mean annual rainfall (520–780 mm/year) for a range of inter-annual rainfall variabilities. Our simulations produced alternative states of grassland and savanna across the mean rainfall gradient. Increasing inter-annual variability had a negative effect on the savanna state under dry conditions (520 mm/year), and a positive effect under moister conditions (580–780 mm/year). The former resulted from the net negative effect of dry and wet extremes on trees. In semi-arid conditions (520 mm/year), dry extremes caused a loss of tree cover, which could not be recovered during wet extremes because of strong resource competition and the increased frequency of fires. At high mean rainfall (780 mm/year), increased variability enhanced savanna resilience. Here, resources were no longer limiting and the slow tree dynamics buffered against variability by maintaining a stable population during 'dry' extremes, providing the basis for growth during wet extremes. Simultaneously, high rainfall years had a weak marginal benefit on grass cover due to density-regulation and grazing. Our results suggest that the effects of the slow tree and fast grass dynamics on tree-grass interactions will become a major determinant of the savanna vegetation composition with increasing rainfall variability.

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1. Introduction

Savannas, biomes with a more or less continuous grass layer and scattered trees (Scholes and Archer, 1997), can be found across a broad range of climatic, edaphic and environmental conditions around the tropics (Lehmann et al., 2011). Rainfall is the primary determinant of maximum tree cover, though actual tree cover can vary due to environmental disturbances such as fire or grazing (Accatino and De Michele, 2016; Sankaran et al., 2005, 2008). Fire limits tree cover by creating a recruitment bottleneck (Bond et al., 2005; Bucini and Hanan, 2007), while grazing can weaken grass competition towards trees by clearing grass cover (D' Odorico et al., 2012; Stevens et al., 2016). Due to such disturbances, savannas can establish under a wide range of climatic conditions, which can be typical for grassland (dry conditions) or forest (wet conditions) (Bond, 2008; Lehmann et al., 2014). These distinct ecosys-

tems which can establish for the same climatic conditions have been described as alternative states (Hirota et al., 2011; Staver et al., 2011a), where thresholds in certain processes govern the dynamics (Beisner et al., 2003).

Among these processes, positive feedbacks play a vital role (D' Odorico and Bhattachan, 2012; Scheffer and Carpenter, 2003). The grass-fire feedback is a case in point: grasses provide the fuel for fires (Bond et al., 2005; Higgins et al., 2000), which hinder the recruitment of young trees into adult ones (Bond and Midgley, 2012; Hanan et al., 2008). Thus, a strong fire disturbance can maintain an open landscape (e.g. grassland) even if the climatic conditions favour forest or savanna (Calabrese et al., 2010; Staver and Levin, 2012). Typically, the strength of this positive feedback will depend on the amount of flammable grass cover and, by extension, tree cover (Archibald et al., 2009; Staver et al., 2011a). If tree cover is sufficiently low, the strong positive grass-fire feedback will force the system to the grassland state, whereas high tree cover will suppress the grass-fire feedback, preserving the forest or savanna state. These two alternative states can be regarded as basins,

each attracting the system towards it, where the aforementioned threshold in tree cover will define the range (or 'radius') of each basin (Nolting and Abbott, 2016). Hence, a state's basin of attraction quantifies the magnitude of a perturbation required to cause a transition from one state to the alternative state (Scheffer et al., 2001), and thus represents the mathematical equivalent to ecological resilience (Holling, 1973). What follows from all of the above is that an external forcing causing changes in the vegetation composition can trigger or suppress a positive feedback with huge implications on the resulting ecosystem (Colombaroli et al., 2014; Scheffer et al., 2009).

Climate change is such an external forcing which is predicted to alter rainfall patterns including inter-annual variability (Fischer et al., 2013; O'Gorman and Schneider, 2009; Wetherald, 2009). Though drylands are expected to be vulnerable to variable rainfall patterns (Ma et al. 2015), we are lacking in knowledge and understanding of this vulnerability (Seddon et al., 2016). Even though it has been shown that trees can suffer from extreme drought (Fensham et al., 2009, 2015), it has also been argued that increasing rainfall variability can benefit trees and shrubs either because of their deeper roots buffering against droughts (Gherardi and Sala, 2015) or via rapid growth episodes in wet years (Holmgren et al., 2006; Holmgren and Scheffer, 2001). However, deeper roots can become less effective under increasingly variable conditions, where a 'temporal niche' may dominate competitive interactions (Xu et al., 2015). Predictions become even harder when environmental factors are considered. In Africa, where fires play a major role in driving savanna dynamics (Staver et al., 2011b), savanna tree cover does not necessarily respond to increased inter-annual rainfall variability (Holmgren et al., 2013), while the impacts of land use could outweigh those of climate change (Aleman et al., 2016). Meanwhile, theoretical studies predict that increasing variability can dampen transitions between alternative states or even eliminate one state in ecological systems in general (Sharma et al., 2014) and drylands in particular (D' Odorico and Bhattachan, 2012). The lack of a consistent pattern across all aforementioned findings starkly demonstrates the need to improve our understanding regarding the drivers of savanna vegetation responses to climatic variability.

With this in mind, we use a theoretical model of savanna dynamics to investigate the impacts of inter-annual rainfall variability on savanna vegetation and resilience, and to understand how tree-grass interactions and the underlying ecological mechanisms shape this response. Our mathematical model is based on the prevailing assumptions on the ecohydrological processes governing African savannas and as such incorporates tree-grass competition, environmental disturbances and feedbacks between trees and grasses as well as between vegetation cover and soil moisture. Using this model, we simulate savanna vegetation under conditions of increasing inter-annual rainfall variability along a gradient of mean annual rainfall.

2. Methods

2.1. Model description

We use the spatially-implicit ordinary differential equations (ODE) model of coupled soil moisture (M), grass cover (G) and tree cover (T) dynamics of (Accatino et al., 2010) as our basis. The coupled equations represent the annual rate of change of each variable:

$$\frac{dM}{dt} = \delta(G, T)\left(\frac{p}{v_1}\right)(1 - M) - \varepsilon M(1 - T - G) - w_G MG - w_T MT$$

(1)

$$\frac{dG}{dt} = c_G MG(1 - T - G) - d_G G - \gamma(G)$$

(2)

$$\frac{dT}{dt} = c_T MT(1 - f(G) - T) - d_T T - \beta(T)$$

(3)

All three variables (M, G, and T) are proportions (ranging between 0 and 1), with M as relative soil saturation, and G and T as fractional cover. The total vegetation cover is limited to 100% ($0 \leq G + T \leq 1$). All simulations were performed using Matlab version R2007b, applying the Matlab ODE solver ode23 to determine the numerical solution of the equations (internal integration time step not fixed, but selected by Matlab to meet a relative error tolerance of 10^{-3}, outputs are then interpolated to the annual level).

Soil moisture dynamics (Eq. 1): Rainfall infiltration is linked with a positive feedback to vegetation cover, $\delta(G, T) = (1 - a)(G + T) + a$. Rainfall, p, is then homogeneously distributed within the unitary volume soil, v_1, and is added to the current soil moisture content. Excess moisture is lost through percolation, $-\delta(G, T)(\frac{p}{v_1})M$, and further losses occur through bare ground evaporation, $-\varepsilon M(1 - T - G)$, and transpiration from grasses and trees, $-w_G MG$, $-w_T MT$ respectively.

Grass cover dynamics (Eq. (2)): Grass cover colonises empty space proportionally to existing cover and soil moisture, $c_G MG(1 - T - G)$. Grass cover is lost due to naturally occurring mortality, $-d_G G$, and grazing, which is an increasing saturating function of grass cover, $\gamma(G) = a_G b^{(1-G)}$. We assume a positive correlation between herbivores and grass cover based on the concept of grazing lawns (McNaughton, 1979).

Tree cover dynamics (Eq. (3)): Density-regulation and fire restrict tree cover expansion, with colonisation being proportional to existing moisture and tree cover, $c_T MT(1 - f(G) - T)$. Fire intensity, $f(G) = \varphi a_S G^{b(1-G)}$, is a sigmoidal function of grass cover (Staver et al., 2011a), and we assume that fire only impacts trees on an annual scale (Staver et al., 2011a). Trees die naturally, $-d_T T$, and cover is also lost due to browsing, $\beta(T) = a_T T^{b(1-T)}$. Browsing only affects tree cover and has been defined similarly to grazing by applying the same reasoning ('browsing hedges', du Toit and Olff 2014).

2.2. Parameters

Those parameters with a 'default' value, common among all simulations (Table 1), are taken from Synodinos et al. (2015), where the model was parameterised to fit the general patterns of savanna tree cover along the rainfall gradient. A maximum rainfall runoff of 25% is assumed in determining the infiltration parameter a (Mwendera and Saleem, 1997). Soils are sandy (porosity 0.4) and we apply a depth of 40 cm, since trees and grasses extract most water from the same shallow depth (Kulmatiski et al., 2010; Kulmatiski and Beard, 2013). The unitary volume soil porosity, v_1, is defined as the product of porosity and depth (Accatino et al., 2010). Evaporation (ε) and transpiration (w_G, w_T) rates are based on the amount of time each process requires to drain the soil of all moisture. We assume that loss of moisture via transpiration occurs slower than via evaporation (Cavanaugh et al., 2011) and that grasses take up water faster than trees per unit area (Graz, 2008). We estimate that evaporation in a bare landscape requires half a year (Mellouli et al., 2000; Wythers et al., 1999), while grass and tree transpiration remove soil moisture in one year and one-and-a-half years respectively. Colonisation rates (c_G, c_T) reflect the time required for each vegetation type to fully colonise an empty landscape uninhibited. Similarly, mortality rates (d_G, d_T) describe the time from full vegetation cover to extinction in the absence of any colonisation. Grasses require half a year to reach full cover and they become extinct after five years (Accatino et al., 2010),

Table 1
Parameter values used as the default parameter set in all simulations (Synodinos et al., 2015).

Parameter symbols and units	Description	Range	Default value
a [-]	Proportion of infiltrating rainfall over bare ground	–	0.75
p [m/year]	Annual rainfall	0.520–0.780	–
v_1 [m]	Unitary volume soil porosity	–	0.16
ε [1/year]	Annual evaporation rate	–	8
w_G [1/year]	Annual rate of grass transpiration	–	6
w_T [1/year]	Annual rate of tree transpiration	–	4
c_G [1/year]	Annual colonisation rate of grasses	–	20
c_T [1/year]	Annual colonisation rate of trees	–	0.2
d_G [1/year]	Annual natural mortality rate of grasses	–	1
d_T [1/year]	Annual natural mortality rate of trees	–	0.023
a_G [1/year]	Maximum annual grazing rate	–	0.7
a_S [-]	Maximum Fire intensity	–	1
φ [-]	Fire Occurrence	Binary 0,1	
a_T [1/year]	Maximum annual browsing rate	–	0.01
b [-]	Non-linear function exponent	–	1.5

while trees require sixty years to reach full cover and two hundred years to become extinct (Accatino et al., 2010; Patrut et al., 2007). The grazing ($\gamma(G)$), fire ($f(G)$) and browsing ($\beta(T)$) functions each have two parameters: a_G, a_S and a_T determine the maximum value for each function respectively, while b determines the slope and is common to all three functions. Maximum grazing and browsing intensities reflect an intermediate disturbance compared to the equivalent natural mortality rates, while maximum fire intensity has not been scaled and is set to 100%. The exponent of these non-linear functions is selected to define a smooth sigmoidal curve (Staver et al., 2011a; Synodinos et al., 2015).

2.3. Rainfall

Rainfall (p in Eq. (1)) is based on a time series of monthly rainfall values aggregated over Kenya, provided by the Climatic Research Unit (CRU) of the University of East Anglia (Harris et al., 2014). The time series spans the years 1901–2012, has a mean value of 650 mm/year and a standard deviation of $\sigma = 12\%$. This annual rainfall value (650 mm) lies on the cusp between resource-limited and moist savannas (Accatino and De Michele, 2016), which are regulated by different processes (Sankaran et al., 2005). To create a gradient that shifts from dry to wet conditions we produce four additional scenarios with mean annual rainfall of ~520, ~580, ~720, and ~780 mm (i.e. 80%, 90%, 110%, 120% of the original). We use the standard deviation of $\sigma = 12\%$ as the basis inter-annual rainfall variability scenario and create a gradient of variability from 0.5σ to 2σ, with an increment of 0.25σ for all mean rainfall conditions. We extend the variability gradient more toward higher values, since the future projections point to that direction (Nicholson, 2000; Wetherald, 2009). Combined with the observation that many parts of Kenya already experience inter-annual rainfall variability greater than 12% (Alemayehu et al., 2017), this is a plausible scenario.

2.4. Fire stochasticity

We simulate the occurrence of fires (Eq. (3)) stochastically. This stochastic occurrence is represented in the fire intensity function, $f(G) = \varphi \, a_S G^{b(1-G)}$, by the fire occurrence factor φ, which takes either the value 0 or the value 1 based on a fire occurrence criterion. This criterion rests on the assumption that the probability of a fire occurring, Pr($fire$), increases linearly with grass cover (Accatino and De Michele, 2013; Beckage et al., 2011; Higgins et al., 2000). Therefore, we have Pr($fire$) $= \alpha G$, where we set $\alpha = 1$. The stochasticity is induced by comparing a random number, r, picked from a uniform distribution between 0 and 1, $r \in U[0, 1]$, to the probability of fire. A uniform distribution was selected to maintain

the linear relationship between fire occurrence and grass cover. If $r \leq$ Pr($fire$), then $\varphi = 1$ and a fire occurs, otherwise if, $r >$ Pr($fire$) then $\varphi = 0$ and no fire occurs. Based on this condition, the higher the grass cover the more likely a fire is to occur, as per our original assumption of the linear dependence of fire occurrence on grass cover.

2.5. Model dynamics

Using the default parameter set, we performed simulations for different rainfall scenarios to test the dynamics of the model. We considered a set of [M, G, T] values to be a steady state if the solution trajectories were consistent between simulation replicates and if these replicates stabilised around the same value (with small oscillations induced by the rainfall variability). For any given amount of rainfall tested the model produced two alternative steady states (bistability), where the attained steady state depended on the initial tree cover (exemplary runs shown in Fig. 1). Thus, we established that the model exhibits steady state dynamics and that alternative steady states exist.

2.6. Biome definitions

Biomes are determined based on the combination of grass and tree cover as in Synodinos et al. (2015). $G < 10\%$ and $T < 10\%$ is classified as desert, while $G \geq 10\%$ and $T < 10\%$ as grassland. Savannas are characterised by $G \geq 10\%$ and $10\% \leq T < 80\%$. If $10\% \leq T < 80\%$ and $G < 10\%$, the biome is classified as a woodland or shrubland, and if $T \geq 80\%$, it is classified as forest, irrespective of grass cover.

2.7. Steady state simulations

We simulate the tree cover steady states along the rainfall variability gradient for our mean rainfall scenarios between 520 mm and 780 mm with initial tree cover values of $T_0 = 5\%$ and $T_0 = 50\%$. Based on the aforementioned test runs, these initial values are appropriate for demonstrating the existence of the two alternative states where they exist. Initial soil moisture and grass cover are the same for all simulations ($M_0 = 10\%$, $G_0 = 10\%$). For each mean rainfall, inter-annual rainfall variability and initial tree cover combination, 50 simulation iterations are performed, with a different rainfall time series per iteration. The required simulation durations are presented in Supporting Table 1, Appendix 6. To minimise the noise induced by the stochasticity, the steady state values we use are the mean value over the final 100 simulation years.

2.8. Bistability threshold range

Since the dynamics are sensitive to initial tree cover, there exists a rainfall-dependent threshold in initial tree cover separating the two alternative states. Given the stochasticity in the model, this threshold is a range rather than a single value, and the initial values within this range do not lead to the same outcome 100% of the time (see Fig. 1b for example). To determine this threshold for each mean rainfall scenario we simulate a range of initial tree cover values along the rainfall variability gradient. We perform 100 simulation iterations per rainfall variability and initial tree cover combination and allow each simulation to reach a steady state. The proportion of simulations which lead to a savanna state is termed as the 'Savanna state probability' or P_S. The contours of the savanna state probability reflect the savanna state's basin of attraction.

2.9. Analysis of mechanisms

To investigate the mechanisms leading to the patterns observed in the results we perform a final set of simulations for semi-arid (~520 mm/year) and mesic (~780 mm/year) conditions under current ($\sigma = 12\%$) and high rainfall variability (2σ) and observe the transient dynamics before steady state is reached (first 500 simulation years). We evaluate grass cover, fire frequency, annual rainfall and the resulting change in tree cover, with a special focus on the impact of extreme dry and wet years in each setting. For this set of simulations we sought initial tree cover values for which the impact of high variability is evident. For semi-arid conditions this means initial tree cover above the current variability tree cover threshold, while for mesic conditions within the bistability threshold for current variability. A value satisfying both conditions is $T_0 = 16\%$. We perform 36 iterations and aggregate all data-points in a single dataset.

2.10. Sensitivity analysis: parameters and modelling assumptions

We perform a local sensitivity analysis to test the response of the three variables towards parameter changes by shifting a single parameter at a time, with all other model parameters remaining at their default values. In the first part of the sensitivity analysis, we perturb each parameter by −20%, −10%, +10% and +20% (Appendix 1). We apply this to the full parameter set, apart from fire intensity, which is tested separately (Appendix 2). We also perform an additional analysis to assess whether trees accessing moisture from deeper soil layers changes the results (Appendix 3). Fur-

thermore, we compare simulation outputs to tree cover data from (Sankaran et al., 2005) (Appendix 4).

3. Results

### 3.1. Alternative states and their basins of attraction

We simulated the tree cover steady states along the inter-annual rainfall variability gradient for our mean annual rainfall gradient. Here we present the results for the two extreme cases: semi-arid (~520 mm) and mesic (~780 mm), while the rest are shown in the Supporting Material (Appendix 7). For current rainfall variability levels, both mean rainfall scenarios produced alternative tree-less grassland and savanna states (Fig. 2).

Under semi-arid conditions (Fig. 2a), there was a gradual reduction of tree cover in the savanna state along the rainfall variability gradient for values between 0.5σ and 1.5σ, starting at *36%* and dropping to 35%, 34%, 32%, and finally 30%. Once variability increased to 1.75σ, the savanna steady state collapsed, eliminating bistability, and producing a single tree-less grassland state. Tree cover in the mesic savanna state barely changed with rainfall variability (Fig. 2b). From one end of the variability gradient to the other (0.5σ-2σ) mesic savanna tree cover only dropped by *2%* (from *58%* to *56%*).

Apart from the steady state values, increasing rainfall variability also impacted the basins of attraction of the alternative states and hence their resilience (Holling 1973). The semi-arid savanna basin of attraction contracted with variability prior to the elimination of the savanna state beyond variability of 1.75σ (Fig. 3a). However, as mean rainfall increased, variability caused the expansion of the savanna basin of attraction (Fig. 3b–e), enhancing the resilience of the savanna state. In the mesic case (Fig. 3e), for example, starting with tree cover at T_0=15%, there was a 10% savanna establishment probability under current variability levels. This probability more than doubled, to *23%*, for double the variability (2σ). The same pattern held along the simulated gradient of initial tree cover values, T_0 (see Appendix 6, Supporting Table 3 for the full results of the mesic basin of attraction).

3.2. Vegetation dynamics and fire

To interpret this contrasting effect of variability on the savanna resilience between semi-arid and mesic conditions we investigated the response of three key variables to annual rainfall: relative change in tree cover between years (Fig. 4), grass cover and fire frequency (Fig. 5). In the semi-arid case, tree cover change was on
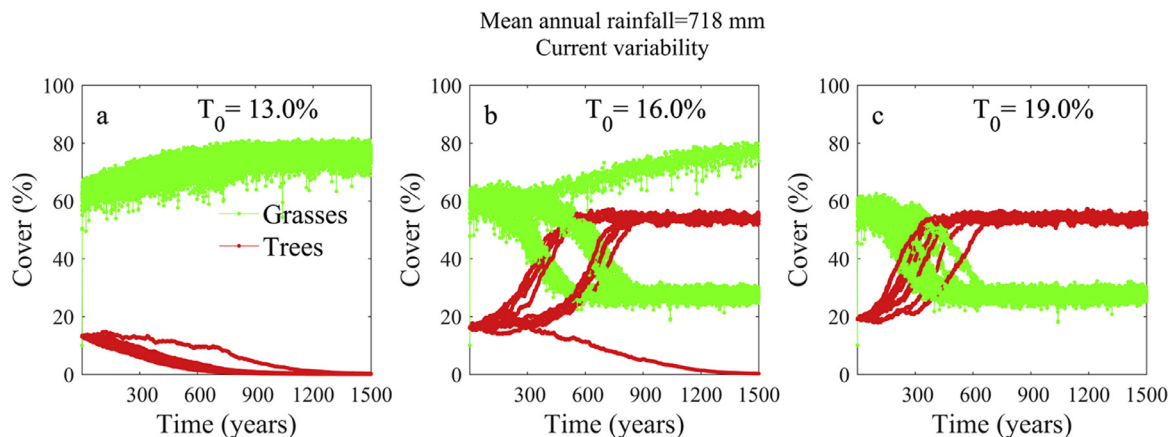
Fig. 1. Grass and tree cover (%) over time for moist conditions (~720 mm/year) and current variability ($\sigma = 12\%$). Each plot shows 10 simulation iterations of a different initial tree cover each time: a) $T_0 = 13\%$, b) $T_0 = 16\%$, c) $T_0 = 19\%$. In the first case tree cover drops to 0%, in the second one there are two possible outcomes (savanna and grassland) since $T_0 = 16\%$ lies within the bistability threshold, and in the third case all simulations converge to the savanna state.
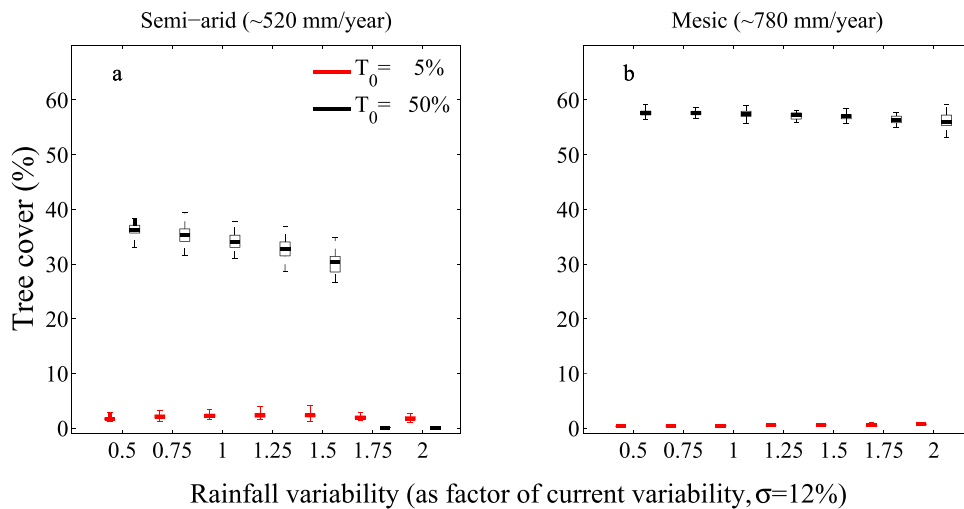
Fig. 2. Alternative states of tree cover along the inter-annual rainfall variability gradient for two mean rainfall scenarios: (a) semi-arid (~520 mm/year); (b) mesic (~780 mm/year). The alternative steady states occur as a result of the different initial conditions: $T_0 = 5\%$ and $T_0 = 50\%$. Each box corresponds to the steady states of 50 iterations with different rainfall time series. All simulations were performed using the default parameter set (Table 1). The semi-arid simulations with low initial tree cover produce outcomes slightly above 0%, even at high variability, because the dynamics have not fully developed within 8000 simulation years. Based on the fact that the simulations with $T_0 = 50\%$ do converge to 0% cover at high variability after 30,000 simulation years we can safely assume that a longer simulation time would result in 0% tree cover for the scenario with low initial tree cover as well.
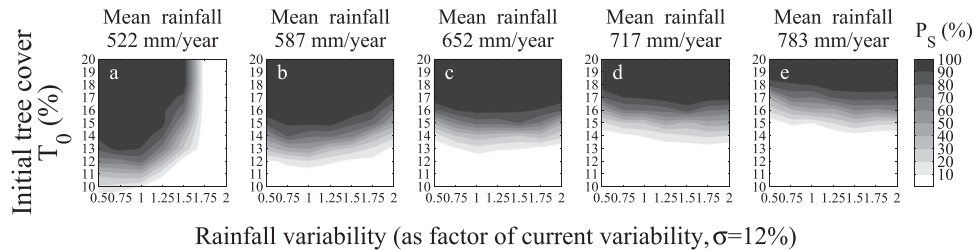
Fig. 3. The basins of attraction of the two states (grassland – white, savanna – black) and the bistability threshold in between along the inter-annual rainfall variability gradient for 5 mean rainfall scenarios: a) ~520 mm, b) ~590 mm, c) ~650 mm, d) ~720 mm, and e) ~780 mm. P_S (%) or 'Savanna state probability' describes the proportion of simulation iterations (100 in total) converging to the savanna state. All simulations were performed using the default parameter set (Table 1).

average negative at the lower end of the rainfall gradient, while with increasing rainfall the change in tree cover became positive for both current and high variability (Fig. 4a). However, despite the positive response to high rainfall (3rd quartile) being of a similar magnitude for both current and high variability levels, the negative impact of the dry extremes (1st quartile) was much stronger in the high variability scenario (Fig. 4c). This asymmetric impact of the extremes in the high variability case meant that tree cover growth in the wet extremes could not compensate for the drop in tree cover during the dry extremes. The stronger effect of the dry extremes in the high variability case can be attributed to a higher frequency of more intense droughts (Fig. 4a, rainfall distribution). However, the fact that a corresponding increase did not materialise in the wet extremes was due to grasses, which have much faster dynamics than trees. This fast responsiveness of grasses meant that grass cover varied significantly with rainfall and fire frequency mirrored this pattern (Fig. 5a). Focusing on the wet extremes (3rd quartile), we found high grass cover. This led to strong direct competition and increased fire frequency (Fig. 5c), thus limiting tree cover growth. Combined with the occurrence of more frequent droughts, increased rainfall variability produced a net negative effect on trees, causing their eventual extinction.

In the mesic case the savanna state was not vulnerable to resource limitation (Fig. 4b, rainfall distribution). Change in tree cover was negative almost throughout the rainfall gradient for current variability, but high variability produced an increasing pattern in tree cover change (Fig. 4b). 'Dry' extremes caused a negligible

negative effect on tree cover under high variability (Fig. 4d) and led to low grass cover (Fig. 5d). The latter negatively impacted the occurrence of fires (Fig. 5d), helping minimise the loss of tree cover in these years (Fig. 4d). During wet extremes, change in tree cover was strongly positive under high variability (Fig. 4d), while grass cover and fire frequency were lower compared to current variability levels (Fig. 5d). The positive impact of wet extremes (and their increased frequency under high variability), allowed tree cover to expand, pushing it above the bistability threshold, and increasing the likelihood of the establishment of the savanna state in the long-term.

4. Discussion

Our ecohydrological model of African savannas produced alternative states of savanna and a tree-less grassland along a rainfall gradient spanning semi-arid and mesic conditions (Fig. 2 and supporting material SF 7) in agreement with observations (Hirota et al., 2011; Sankaran et al., 2005). Tree-grass coexistence was the result of competition alone, with fire limiting tree cover below the rainfall-determined maximum (Appendix 5), consistent with our understanding of savanna dynamics (Bucini and Hanan, 2007; Higgins et al., 2010; Sankaran et al., 2008). Moreover, as repeatedly argued (Bond, 2008; Staver et al., 2011a; van Langevelde et al., 2003), the positive grass-fire feedback produced the alternative states, creating a tree cover threshold, which separated the basins of attraction of the two states (Fig. 3). Even though certain models suggest that these states are rarely attained in nature and that sa-
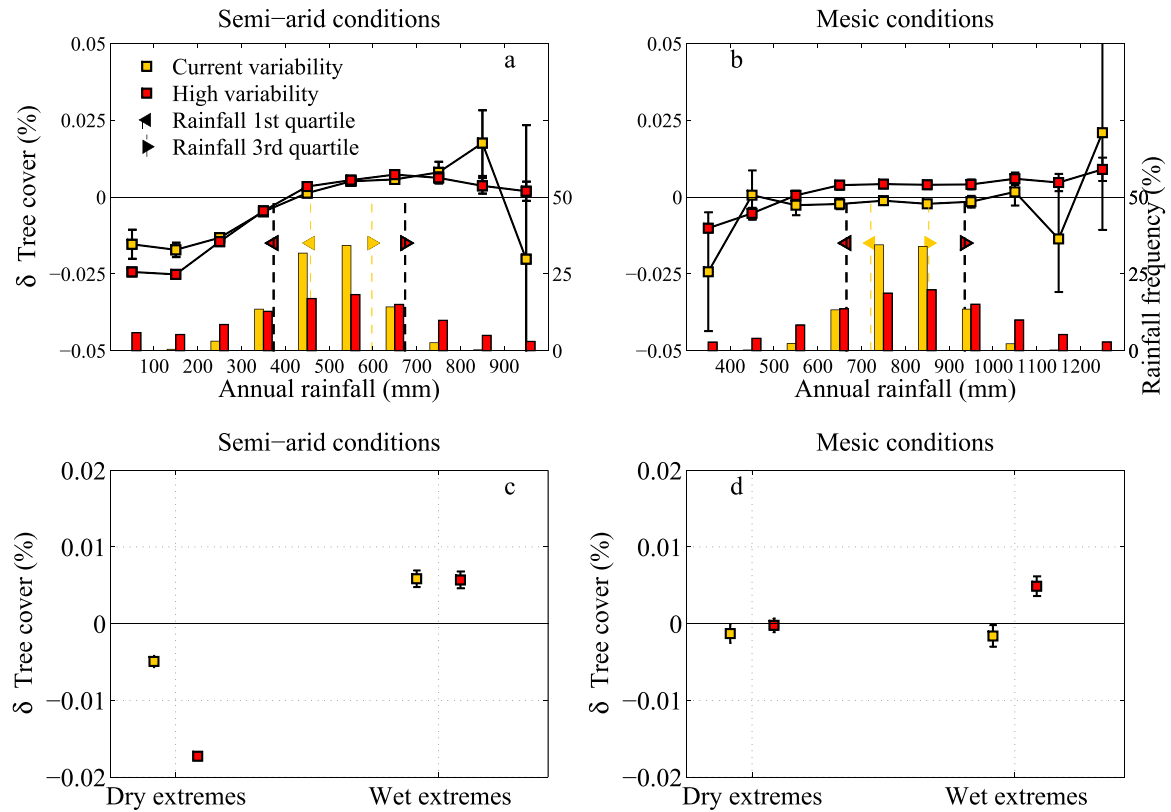
Fig. 4. Relative change (with respect to the previous year) in tree cover in response to annual rainfall for (a) semi-arid (~520 mm) and (b) mesic (~780 mm) conditions; mean relative change in tree cover during extreme dry (1st quartile of the rainfall distribution) and wet (3rd quartile of the rainfall distribution) years for (c) semi-arid and (d) mesic conditions. Points represent mean values with error bars from 36 simulations. The rainfall values along the x-axis are plotted as a distribution with relative frequency shown on the right-hand y-axis. The perpendicular dashed lines show the 1st (left arrow) and 3rd (right arrow) quartiles of each rainfall distribution.
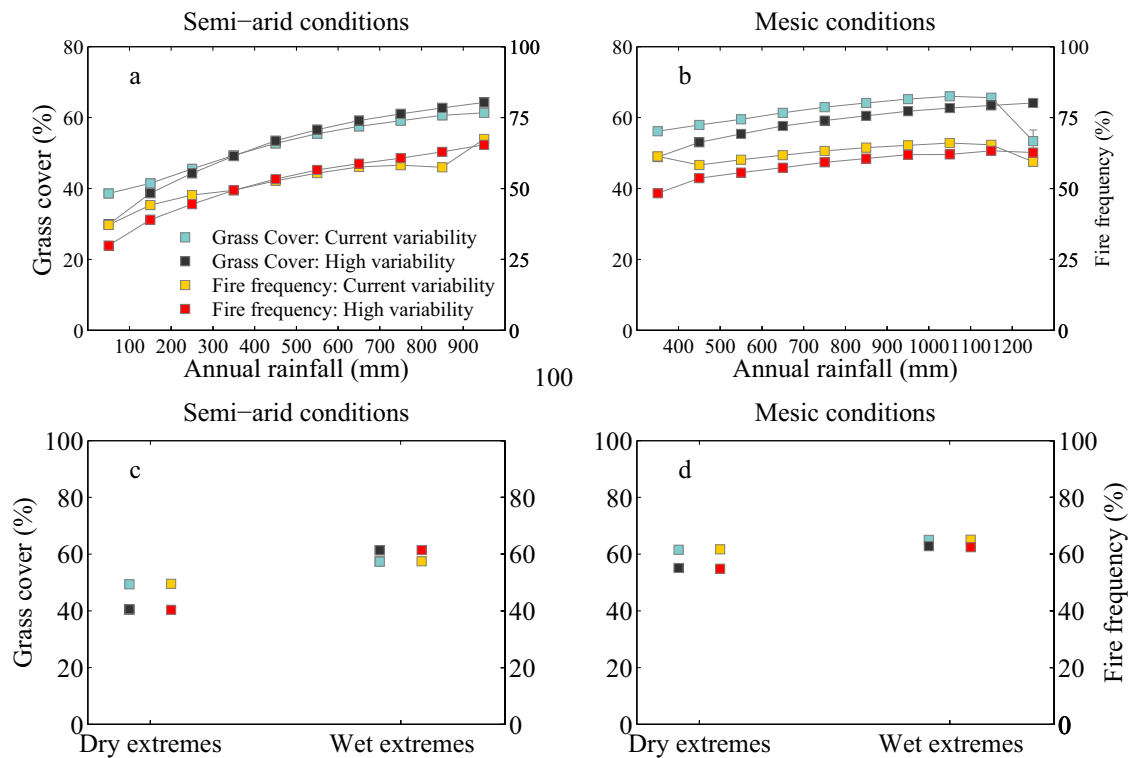
Fig. 5. Mean grass cover and fire frequency values for different amounts of annual rainfall: a) semi-arid (~520 mm) conditions rainfall gradient, b) mesic (~780 mm) conditions rainfall gradient, c) semi-arid rainfall extremes (1st and 3rd quartiles of rainfall), and d) mesic rainfall extremes. The points are derived from 36 simulation iterations. The legend in (a) applies to all four plots.

vannas represent inherently unstable (Jeltsch et al., 2000) or transient states (Accatino and De Michele, 2013, 2016), our focus is on the underlying dynamics and rainfall variability's effect on tree cover (and by extension the savanna state) rather than the stability of savannas. The novelty of our study lies in the investigation of the impact of increasing inter-annual rainfall variability on tree-grass coexistence and the resilience of the savanna state. We found that increasing variability had a contrasting impact on savannas depending on the mean rainfall amount, a result which we discuss below.

4.1. The contrasting impact of rainfall variability

In the semi-arid scenario (∼520 mm/year), increasing variability had a negative effect on savanna tree cover and the savanna state overall, as opposed to moister conditions (≥ 580 mm/year), where variability enhanced the resilience of the savanna state. More specifically, under semi-arid conditions high variability led to the extinction of trees and the elimination of the savanna state (Fig. 2a). Leading up to this, the basin of attraction of the semi-arid savanna state gradually contracted along the variability gradient (Fig. 3a). Such an elimination of one alternative state or the contraction of its basin of attraction as a result of increasing variability has also showed up in theoretical studies of other bistable ecological systems (Ai et al., 2003; Rong et al., 2012), particularly when the variability was uncorrelated (Sharma et al., 2014) as in our simulations. The same phenomenon occurred in studies specific to dryland dynamics, with bistability being eliminated due to stochasticity (D'Odorico et al., 2005; D'Odorico and Bhattachan, 2012; Guttal and Jayaprakash, 2007).

In our simulations, high variability caused the loss of the semi-arid savanna state through a combination of more frequent droughts and stronger direct (resources) and indirect (fires) competition from grasses towards trees. In years of extreme aridity, tree cover dropped, while in wet years tree cover responded positively (Fig. 4c). The key was that the gain in the latter case was not as big as a loss in the former, producing a net negative effect of extreme rainfall events on tree cover. As variability increased, so did the frequency of these extremes, eventually leading to the extinction of trees. Even though it has been argued that the deeper tree roots could shield trees against variability (Gherardi and Sala, 2015), there exists evidence that trees cannot always withstand droughts, particularly when these are extreme (Fensham et al., 2009, 2015) as was the case in our simulations (Fig. 4a, c). Even when we accounted for trees being able to access soil moisture from depths beyond the reach of grasses, the negative impact of rainfall variability on trees persisted, albeit having shifted towards drier mean rainfall conditions where resources were limited for trees despite their additional water uptake (Appendix 3). Compounding the negative impact of droughts was the inability of trees to compensate with sufficient growth during extreme wet years (Fig. 4c) with grasses being the main reason behind this. The rapid response speed of grasses meant that competition was strongest during years of high resource availability, a common phenomenon in savannas (February et al., 2013; Riginos, 2009). Apart from grasses limiting the ability of trees to access water, high grass cover also resulted in more frequent and intense fires (Fig. 5a, c), a positive feedback that hampered tree recruitment (Bond, 2008; Staver et al., 2011b) and one which was missing in the aforementioned study of Gherardi and Sala (2015). Tellingly, in a study based on satellite data (Holmgren et al., 2013), tropical savanna trees generally responded positively to increasing rainfall variability, but African sites did not follow this pattern with fire being touted as a possible reason for this. In our simulations, high rainfall variability favoured grasses due to their fast responsiveness, which increased the frequency and intensity of fires. This stronger

impact of fires ultimately hindered tree cover recovery and growth, essentially supporting the idea of Holmgren et al. (2013).

On the other hand, mesic savannas (∼780 mm/year) became more resilient with increasing rainfall variability (Fig. 3e). The lack of resource limitation minimised the impact of 'dry' extremes on tree cover and during wet extremes, there was sufficient water to promote tree colonisation episodes irrespective of the occurrence of fires (Figs. 4d, 5d). These episodes resemble what Harrington, (1991) described as pulses where the balance between moisture availability and the fire disturbance favours tree establishment, considered essential for tree survival. Holmgren and Scheffer, (2001) termed these extremely wet years as 'windows of opportunity' where tree cover could rapidly expand, as confirmed in a later study (Holmgren et al., 2006). At the same time, the marginal benefit of high rainfall to grasses decreased (Appendix 8, SF8). High pre-existing grass cover induced strong density-regulation, and increased the strength of the negative grazing feedback, while the simultaneous increase in tree cover triggered stronger competition. A consequence was the reduction in the frequency of fires (Fig. 5b, d), further improving the conditions for the expansion of tree cover. Under high levels of rainfall variability, the frequency of such windows of opportunity for tree cover growth increased, allowing tree cover to move above the bistability threshold and, thus, enhancing the resilience of the mesic savanna state.

4.2. Plant responses to increasingly variable conditions

This is not the first study to find that the impact of variability in an external forcing can change depending on the mean value of the system's main driver (Martin et al., 2016). In our case, variability of rainfall under water-limited conditions impacted direct plant-plant interactions by intensifying resource competition. These conditions did not favour the slow-responding trees, which were not only outcompeted by grasses for resources, but their growth was further limited via fire. Bond et al. (2003) showed how post-burn tree growth rates were a major factor in determining whether savanna trees would survive or not, albeit with atmospheric CO_2 driving these rates. Hence, it is possible that responding fast to variable conditions will become the defining aspect of plant interactions in resource-limited environments, making temporal processes and corresponding plant traits the major driver of dynamics (Hoover et al., 2014). Xu et al. (2015) demonstrated this quite elegantly in a study of increasing rainfall intensities in savannas. Despite the general expectation that trees would benefit from more intense rainfall events due to increased percolation (Kulmatiski and Beard, 2013; Mazzacavallo and Kulmatiski, 2015; Ward et al., 2013), Xu et al. (2015) showed how grasses would actually be the beneficiaries due to their aggressive water use strategy. Response speed was the defining factor in our results too: grasses were too fast for trees in semi-arid conditions, competing stronger and fuelling more fires in years of high rainfall. In mesic conditions, where even in the low rainfall years resources were not limited, the slow dynamics of trees worked in their favour. By absorbing the stress of rainfall variability and maintaining a fairly stable population, trees could take advantage of the favourable conditions in years with high rainfall. Similarly to the process of the 'storage effect' (Higgins et al., 2000), opportunistic tree growth counteracted variability and proved vital for the savanna establishment.

4.3. Open questions

We modelled rainfall variability without auto-correlation between years. Theoretical studies show that this can impact how bistable systems respond to variability (Ai et al., 2003; Sharma et al., 2014), which is relevant due

to the link between rainfall patterns and the El Nino Southern Oscillation cycle (Holmgren and Scheffer, 2001). Furthermore, high rainfall variability could be linked to more intense individual rainfall events (Easterling et al., 2000; O' Gorman and Schneider, 2009). Both our work and that of Xu et al. (2015) demonstrated that the tree advantages due to root niche separation (Gherardi and Sala, 2015; Kulmatiski and Beard, 2013), may fail under high rainfall variability and intensity. Future studies of higher complexity would be required to address this and enhance our understanding. Fire could also be affected by climatic and environmental variability, particularly with respect to the timing of fires within a year (Nelson et al., 2012). Even though our analysis (Appendix 2) demonstrated that stochasticity in fuel load did not counteract the impacts of increasing variability, more targeted studies should address the specifics of fire dynamics. This issue is also linked to the discretisation of time within a model. We solved our time-continuous differential equations using discretisation time steps of variable lengths in order to satisfy our accuracy criteria. Even though the impact of fire may have varied with the length of each discretisation interval, all these time steps were less than a year long, so their effect could not have been disproportionately large. Nevertheless, when fire was applied within a fixed-length (one year) discrete-time approach it created greater variability between years (e.g. Accatino and De Michele 2013; Baudena et al. 2010).

5. Conclusions

Our study showed how the impact of increasing rainfall variability on savannas changed with mean rainfall. In semi-arid conditions, rainfall extremes had a net negative effect on tree cover; high variability made these extremes more frequent and trees lost out. The loss of tree cover occurred because the slow responsiveness of trees prevented them from acquiring adequate resources as grasses outcompeted them and fueled more fires. In the mesic case, the slower tree dynamics provided a buffer against stochasticity by maintaining a stable population which could take advantage of high-rainfall years. Thus, opportunistic tree growth became more beneficial under high variability. Future studies should aim to further test how variability impacts plant interactions, using existing insights provided here and in other studies as building blocks where appropriate. The idea of a temporal niche deserves a thorough investigation, as it may provide a solid conceptual framework for studying plant responses to climatic variability.

Authors' contributions

ADS conceived of the study, developed the model, and ran the simulations and analyses. FJ and BT helped during the model development. DL contributed to the development of appropriate figures. All authors participated in the preparation of the manuscript. All authors gave final approval for publication.

Data availability: The study consists of model outputs. The model is extensively described in the 'Methods' so that any reader can reproduce the results of the study.

Competing interests: We have no competing interests.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jtbi.2017.10.019.

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